Large-Scale Effects of Timber Harvesting on Stream Systems in the Ouachita Mountains, Arkansas, USA

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ABSTRACT / Using Basin Area Stream Survey (BASS) data from the United States Forest Service, we evaluated how timber harvesting influenced patterns of variation in physical stream features and regional fish and macroinvertebrate assemblages. Data were collected for three years (1990–1992) from six hydrologically variable streams in the Ouachita Mountains, Arkansas, USA that were paired by management regime within three drainage basins. Specifically, we used multivariate techniques to partition variability in assemblage structure (taxonomic and trophic) that could be explained by timber harvesting, drainage basin differences, year-to-year variability, and their shared variance components. Most of the variation in fish assemblages was explained by drainage basin differences, and both basin and year-of-sampling influenced macroinvertebrate assemblages. All three factors modeled, including interactions between drainage basins and timber harvesting, influenced variability in physical stream features. Interactions between timber harvesting and drainage basins indicated that differences in physical stream features were important in determining the effects of logging within a basin. The lack of a logging effect on the biota contradicts predictions for these small, hydrologically variable streams. We believe this pattern is related to the large scale of this study and the high levels of natural variability in the streams. Alternatively, there may be time-specific effects we were unable to detect with our sampling design and analyses.

The relationships between stream organisms and their habitats are complex and vary depending on spatial, temporal, or taxonomic scale (Angermeier 1987, Schlosser 1987, Lammert and Allan 1999). From results of studies in a variety of systems, many investigators have argued that physical variability structures aquatic communities (Gorman and Karr 1978, Grossman and others 1982, Freeman and others 1988, Delucchi and Peckarsky 1989, Grimm and Fisher 1989, Capone and Kushlan 1991, Jackson and Harvey 1993, Taylor and others 1993, Williams and others 1996). Most of these studies focused on one group of organisms, in one system, and over limited temporal and spatial scales. Few studies have examined how fish and macroinverte-

brate assemblages are structured with respect to habitats at larger scales (Jackson and Harvey 1993).

Describing the relationships between aquatic organisms and their habitats is a major goal of the United States Forest Service (Overton and others 1993). Managers increasingly have used basin-wide estimation techniques (Hankin and Reeves 1984) to inventory assemblages and habitats within drainage basins. Using the Hankin and Reeves (1984) model, the Ouachita National Forest conducted Basin Area Stream Surveys (BASS) in six paired streams contained within three hydrologically variable drainage basins in Arkansas, USA, during 1990–1992 (Clingenpeel and Cochran 1992). We used the paired-basin design (Ponce and others 1982) of these surveys to better understand the geographical variation in regional aquatic assemblages and habitats.

We used multivariate techniques to identify important sources of variability in regional fish and macroinvertebrate assemblages and physical stream features. Specifically, we asked how year-of-sampling, drainage basin level environmental factors, and presence or ab-

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sence of timber harvest within a drainage basin influenced stream habitat, water chemistry, and regional assemblage structure (based on taxonomy and trophic affiliation) of fishes and macroinvertebrates. With this design, we assessed the efficacy of BASS methodology for detecting large-scale effects of timber management.

Temporal variability in physical stream features can influence the structure of animal assemblages, particularly in streams strongly influenced by periodic droughts and floods (Delucchi and Peckarsky 1989, Grimm and Fisher 1989, McElravy and others 1989, Capone and Kushlan 1991). Historical factors, such as biogeographic history and geomorphology, also interact with contemporary ecological processes to influence the organization of assemblages (Matthews and Robison 1988, Ricklefs and others 1999).

The effects of forest management practices on fishes in central United States streams are largely unknown (Hicks and others 1991, Rutherford and others 1992, Brown and Matthews 1995). Most studies have been conducted at limited spatial and taxonomic scales (i.e., one group of organisms within individual stream reaches) and most have been conducted in coldwater trout streams in the western United States (Hicks and others 1991, Rutherford and others 1992). Macroinvertebrates in forested mountain streams are particularly susceptible to timber harvesting activities because of their association with stream habitats and riparian zones (Webster and others 1992, Wallace and others 1997). Timber harvesting can lead to short-term changes in community composition of macroinvertebrates (Campbell and Doeg 1989, Allan 1995), and persistent sedimentation caused by logging roads may have long-term effects on macroinvertebrate assemblages (Silsbee and Larson 1983, Campbell and Doeg 1989). In this study, we attempted to address the effects of timber harvest on regional fish and macroinvertebrate assemblages at the drainage basin scale.

Methods

Study Area

The six study streams are within the drainage basins of the Arkansas, Saline, and Cossatot rivers in the Ouachita Mountains, Ouachita National Forest, Arkansas, USA (Table 1). The Ouachita Mountains, located in southeastern Oklahoma and southwestern Arkansas, consist of east–west-oriented ridges and valleys. Rivers in the uplifted areas are crooked, with cliffs and gorges along stream valleys (Fenneman 1938, Robison 1986). South Alum and Bread creeks are located in the east-central subsection of the Ouachita Mountains, and

Table 1. Streams sampled by the USDA Forest Service in 1990–1992 in Ouachita National Forest, Arkansas, USA[a]

Stream	Basin	Area (ha)	Mgmt
South Alum	Saline R.	1533	R
Bread	Saline R.	1517	M
Caney	Cossatot R.	2518	R
Brushy	Cossatot R.	3428	M
Dry	Arkansas R.	2170	R
Jacks	Arkansas R.	2938	M

[a]Reference streams indicated by an "R" and managed forest by an "M".

Brushy and Caney creeks are within the Athens Piedmont Plateau subsection (Keys and others 1995). Jack and Dry creeks are within the Fourche Mountain subsection, located along the northern edge of the Ouachita Mountains (Keys and others 1995).

Many small streams in the Ouachita Mountains have a highly variable flow regime throughout the year (Brown and Matthews 1995, Taylor 1997). Much of the flow in these streams is maintained by rainfall events. As a result, streams often dry to isolated pools in the summer months, while the steep gradient of these streams produces high-velocity floods during periods of heavy rainfall. These periodic oscillations in flow can have a strong influence on stream biota (Taylor and others 1993), and several sensitive and/or endemic species are found in these streams (Robison and Buchanan 1988).

Streams within each drainage basin were paired, according to Ponce and others (1982), with one stream in a basin managed for timber and one with no harvesting activities (Table 1). The extent of timber harvest activities over the last 100 years is reflected in age-class distributions of trees within the basins (Table 2). Relative to reference basins, managed ones show higher areal percentages of forest in early succession and a lower percentage of mid- to late-successional forest (Table 2). In addition, managed stream systems are much more impacted by road networks, including more road crossings, higher road densities, and closer proximity to streams (Table 2). In general, managed basins in the Ouachita National Forest are a mosaic of stand types ranging from small clear-cuts to old-growth stands. A variety of harvesting practices are used in these basins, including: even-age methods (seed tree and shelterwood), uneven-aged methods (single-tree and group selection), and temporary wildlife openings. Unharvested (reference) basins are also a mosaic of stand ages, but natural processes dictate the structure of these stands.

Table 2.   Differences among reference and managed basins[a]

Stream	Age (yr)				Road crossings (N)	Road density (m/ha)	%33	%100
	0–30	31–50	51–80	81–150				
S. Alum	2.8	12.9	37.1	37.8	7	1.47	2.21	8.55
Bread	13.2	5.3	55.8	15.7	8	1.61	5.99	35.97
Caney	0	0	36.1	63.9	0	0.07	0	0
Brushy	20.2	2.7	43.7	25.9	22	0.76	18.09	43.07
Dry	0.7	15.2	61.5	21.4	2	0.59	0.76	2.50
Jack	16.3	0.4	61.8	16.6	22	1.08	4.75	21.62

[a]Shown are age classes of tree stands, number of road crossings on the streams, road density percent of road network in a basin within 33 m of the stream (%33), and percent of the road network within 100m of the stream (%100).

Sampling Methods

USDA Forest Service inventory teams (led by J.A.C.) surveyed each stream. All members of inventory teams were trained by J.A.C., and every attempt was made to standardize and validate data collection techniques among the groups. These teams classified habitat units (i.e., dry channel, low-gradient riffle, high-gradient riffle, cascade, secondary channel pool, backwater pool, trench/chute, plunge pool, lateral scour pool, dammed pool, glide, run, step-run, mid-channel pool, edgewater, channel confluence pool, pocket water, corner pool, step pool, and bedrock sheet) according to McCain and others (1990). The teams classified habitat units for each stream from the lower portions to the headwaters. This method provided a comprehensive coverage of the total area of each stream. All data were collected in 1990–1992 from late May to early August.

Inventory teams measured physical variables within each habitat unit. Teams measured width, thalweg depth, and average stream depth along a transect at the midpoint of each unit. Substrate composition was visually estimated as the percentage of six size classes (i.e., bedrock, boulder, cobble, gravel, sand, and clay/fine sediments). Embeddedness was estimated as the average percent of cobble surrounded by fine sediments (Clingenpeel and Cochran 1992). Teams estimated several in-stream cover variables as the percentage of area occupied: undercut banks, large woody debris, small woody debris, terrestrial vegetation overhanging the stream, whitewater, boulder ledges, vegetation clinging to the substrate, and rooted vegetation (Clingenpeel and Cochran 1992). A clinometer was used to estimate bank angle, and bank stability was estimated as the percentage of the bank that was not eroded (Clingenpeel and Cochran 1992). Canopy closure was measured with a spherical densiometer at the center of each habitat unit.

Inventory teams collected water chemistry data in 10% of each type of habitat unit (e.g., if 300 mid-channel pools were present in a stream, 30 were sampled at random). These collections were stratified longitudinally along the length of the streams (Clingenpeel and Cochran 1992). Teams measured dissolved oxygen and temperature in the field with a digital meter. Water samples from each site were analyzed for conductivity, pH, bromide, nitrate, phosphorus, manganese, magnesium, sodium, cobalt, calcium, and sulfate. Analyses were conducted at the Northeastern Forest Experiment Station at Berea, Kentucky, USA, with 1983 EPA Methods for Chemical Analysis of Water and Wastes.

The teams also collected organisms in 10% of the habitat units (also chosen at random), and collections were arrayed longitudinally along the stream gradient. Fishes were collected with multiple-pass electrofishing and block nets (Van Deventor and Platts 1985), preserved in 10% formalin, identified, counted, and deposited in the Northeastern Louisiana University Museum of Zoology. A 5-min, kick-net sample was used to collect aquatic macroinvertebrates in all identifiable microhabitat types. In addition, dip-nets were placed downstream and stream substrates were scrubbed for 5-min with a soft bristle brush. Debris collected in the nets also was washed to remove any remaining invertebrates (Clingenpeel and Cochran 1992). Samples from kick-netting and substrate washing were pooled, preserved in 70% EtOH, and identified and counted at Arkansas State University. Macroinvertebrates (mostly insect larvae) were identified to the lowest taxonomic resolution possible, genus in most cases.

Statistical Methods

We summarized stream habitat and water chemistry characteristics for each stream by year and computed means for all measured variables and an overall mean and coefficient of variation for depth measurements. We used 39 physical variables in a principal components analysis (PCA) to reduce the dimensionality of the data matrix to a few significant axes. Eigenvalues for each axis were compared to a broken-stick model to
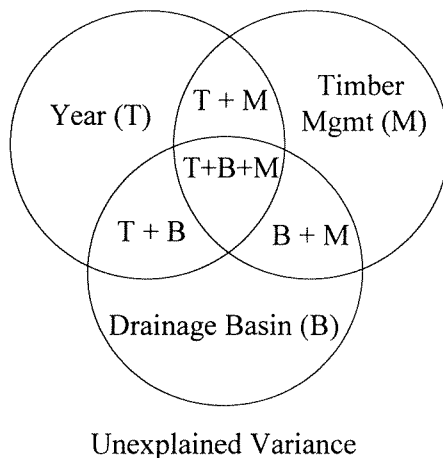
Unexplained Variance

Figure 1. Diagram illustrating how biotic variability was partitioned into three explanatory variables and their shared variance components using canonical correspondence analysis. The boxed region, excluding the overlapping circles, represents the variability not accounted for with these variables.

Table 3. Sorted principal component loadings of the first two axes for environmental and chemical variables, listed by decreasing order of importance for axes[a]

Variable (% variance explained)	Axis 1 (20.8%)	Axis 2 (18.1%)
pH	**0.845**	0.158
Conductivity	**0.835**	0.141
Bromide	**0.834**	−0.020
Canopy closure	**−0.797**	0.187
Riparian vegetation	**−0.776**	0.208
Calcium	**0.713**	0.383
Alkalinity	**0.693**	0.213
Sulfate	**0.631**	0.160
Magnesium	**0.591**	0.311
Cobalt	**−0.555**	0.288
CV depth	**0.543**	−0.042
Rooted vegetation	**−0.517**	0.419
Boulder	−0.189	**−0.863**
Left bank angle	0.229	**−0.732**
Right bank angle	0.267	**−0.716**
Whitewater	−0.119	**−0.679**
Potassium	0.468	**−0.657**
Boulder cover	−0.408	**−0.650**
Gravel	0.046	**0.609**
Temperature	0.118	**0.597**
Dissolved oxygen	−0.005	**−0.591**
Embeddedness	−0.100	**0.565**

[a]Those variables with a correlation of at least 0.50 with axis 1 or 2 are shown in bold type.

determine the interpretability of each axis (Jackson 1993). We used a randomization factorial analysis of variance (Manly 1997) on the interpretable principal components to determine how year-of-sample, drainage basin differences, and the presence or absence of timber harvest in a drainage basin influenced patterns of variation in the physical characteristics of these streams.

We also summarized fish and macroinvertebrate data for each stream by year. For taxonomic analyses, fishes were analyzed by species, and invertebrates were analyzed by genera (or order/family when genus was not determined). We classified invertebrates and fishes into trophic groups according to Allan (1995), after Merritt and Cummins (1984) and Horwitz (1978).

We used a multivariate variance partitioning technique (Borcard and others 1992, Magnan and others 1994, Aude and Lawesson 1998) to relate variation in regional assemblages (taxonomic and trophic) to year of sampling, drainage basin differences, the presence/absence of harvest activities, and their shared variation that could not be partitioned into pure effects (Figure 1). These analyses were based on a series of partial canonical correspondence analyses (CCA) (ter Braak 1986, 1990). CCA is a direct-gradient analysis technique (ter Braak and Prentice 1988) for determining the relationship between species × site or trophic groups × site matrices (separately for fishes and macroinvertebrates) and "dummy" variables (ter Braak 1990) representing year, basin, and timber harvest. We used Monte Carlo tests (10,000 permutations) to estimate the significance of each variable (ter Braak 1990).

We used a multivariate approach to data analyses because these types of tests are more robust to "messy" data (Palmer 1993). We felt this type of an approach was more powerful than using multimetric index methods (e.g., IBI and B-IBI) to analyze the data. With multivariate analyses we were able to assess not only timber harvesting effects, but also how these effects compare with other sources of variability (i.e., differences among the basins and temporal variability).

Results

When eigenvalues of individual principal component (PC) axes were compared with those predicted by the broken stick model (Jackson 1993), only the first two axes were interpretable. Of the 39 physical variables used in the PCA, 20 (51%) had their highest loading on these first two axes, which cumulatively accounted for about 40% of the total variation in the physical data (Table 3). Each of these axes showed a different response to year, drainage basin factors, and timber harvesting (Table 4). Sites ordered along the first principal component were influenced significantly by interactions between basin and logging and basin and year, plus main effects for all three variables (Table 4). This

Table 4. F values from randomization factorial analysis of variance on first two principal components[a]

Factor	Axis	
	PCA I	PCA II
Basin	246.99***	313.43***
Logging	45.73**	0.71
Year	8.03*	35.48**
Basin × logging	10.03*	35.31**
Basin × year	12.61*	7.55*
Logging × year	1.53	1.01

[a]Factors included in the analyses were drainage basin differences, presence or absence of logging in a watershed, and year-of-sample. Significance (P value) is indicated as follows: *0.05, **0.01, ***0.001.

axis was primarily a gradient of water chemistry (i.e., pH, conductivity, alkalinity, and several individual chemical measures) and riparian vegetation characteristics (Table 3). Sites ordered along the second component were related significantly to basin-logging and basin-year interactions, plus basin and year main effects (Table 4). Physicochemical variables (i.e., potassium, temperature, and dissolved oxygen) and measures related to substrate composition comprised the majority of variation in this axis (Table 3).

Over the three years of the study, forest inventory teams collected a total of 30 species of fishes in nine families (Appendix A). Dominant families included Cyprinidae, Percidae, and Centrarchidae. The greatest numbers of individuals were collected in streams of the Cossatot River basin, and species richness was higher in the managed streams than in their paired reference for all three basins (Williams and others 2001). Teams also collected 152 genera of macroinvertebrates in 65 families and 20 orders (Appendix B). Dominant orders included Coleoptera, Ephemeroptera, Diptera, and Trichoptera. As with fishes, streams in the Cossatot River basin had higher densities of individuals. In two of three cases (Saline and Arkansas basins), richness of families was greater in the managed streams than the paired reference (Williams and others 2001). Examples of all major trophic groups of fishes and macroinvertebrates (Horwitz 1978, Merritt and Cummins 1984, Allan 1995) were represented in these data.

Drainage basin differences explained a significant amount of the total variation in regional fish and macroinvertebrate assemblages, whether grouped taxonomically or by trophic group (Figure 2). For macroinvertebrates, year of sample also explained a significant amount of variation for both groupings. Interestingly, year explained more variation than drainage basin for macroinvertebrate trophic assemblages (Figure 2). None of the shared variance components

were significant (Figure 2). For both groups of organisms, whether grouped taxonomically or trophically, we accounted for greater than 50% of their variation with the explanatory variables that were modeled.

Discussion

Many stream systems are subjected to a dynamic natural disturbance regime (Peckarsky 1983, Ross and others 1985, Matthews 1986, Matthews and others 1988, Grimm and Fisher 1989). Because of their naturally high level of disturbance (e.g., variation in flow regime), small streams are a good model system to examine patterns of stability and variability in assemblage structure (Grossman and others 1990). Describing and understanding the variability in stream systems is difficult because processes and patterns vary at different spatial and temporal scales (Wiens and others 1986, Roth and others 1996, Lammert and Allan 1999). Assemblages can vary at small spatial scales yet appear stable, or at least resilient, at larger scales (Rahel 1990). This phenomenon has been referred to as the shifting mosaic, steady-state model (Clark 1991, Moloney and Levin 1996). Studies based on different temporal scales also can produce different results (Wiens and others 1986, Minshall 1988, Ward 1989), particularly in systems that experience environmental extremes at irregular intervals.

Small streams in the Ouachita Mountains are hydrologically dynamic systems. In many of these streams, flow is maintained primarily by precipitation runoff, so there is little capacity to dissipate some of the severe effects of flooding or drought. Perturbations from timber harvesting or other anthropogenic sources may exacerbate this variation and lead to increased variability in assemblage structure over time (Schlosser 1991). Silvicultural activities can lead to increased water temperature, sedimentation, debris accumulation, suspended solids, dissolved ions, and nutrient levels or alter the riparian vegetation structure of streams (Campbell and Doeg 1989). These types of disturbances to the riparian zone potentially disrupt stream-level processes throughout entire basins (Vannote and others 1980, Campbell and Doeg 1989).

We determined that timber harvesting activities in a basin had measurable effects on physical variables but little influence on regional fish and macroinvertebrate assemblages. Most effects of timber harvesting on habitat and water chemistry variables were related to interactions between drainage basins and logging activities (on both axes 1 and 2; Table 4). This seems to indicate that drainage basins differ in their response to logging, and some individual streams are more affected by these
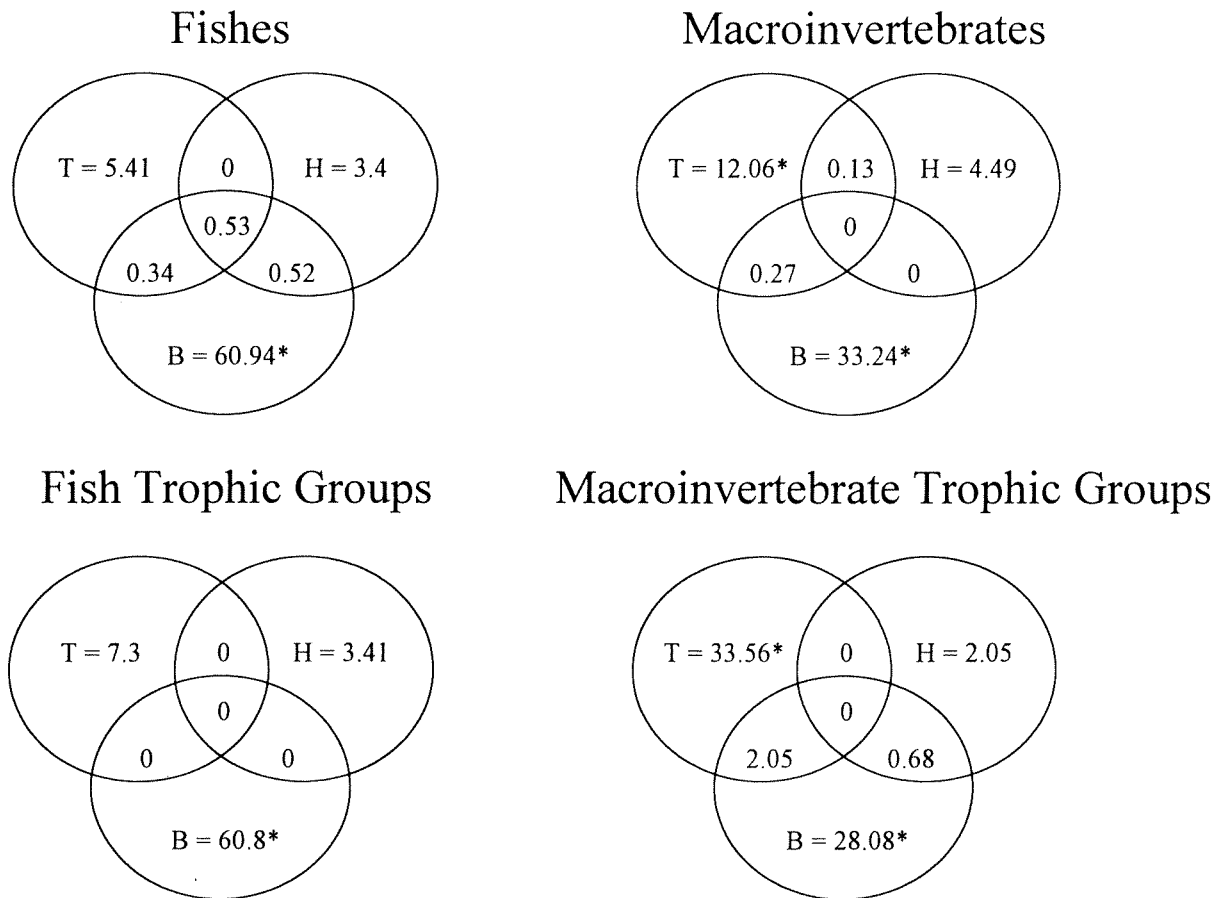
Fishes

T = 5.41 | 0 | H = 3.4
0.53
0.34 | 0.52
B = 60.94*

Macroinvertebrates

T = 12.06* | 0.13 | H = 4.49
0
0.27 | 0
B = 33.24*

Fish Trophic Groups

T = 7.3 | 0 | H = 3.41
0
0 | 0
B = 60.8*

Macroinvertebrate Trophic Groups

T = 33.56* | 0 | H = 2.05
0
2.05 | 0.68
B = 28.08*

Figure 2. Amount of biotic variation, expressed as percentage, explained by (T) year of sample, (B) drainage basin differences, (H) the presence or absence of timber harvesting activities within a watershed, and their shared variance components. The letter (U) represents the variance that could not be accounted for with these variables. *significance ($P < 0.05$) with a Monte Carlo test.

disturbances than others. Alternatively, this could be the result of differences in logging intensity among the drainage basins. Variability in the two PC axes was dominated by water chemistry variables, riparian vegetation characteristics, and substrate composition. These patterns are consistent with previous studies that have alluded to the influence of timber harvesting on these types of variables (reviewed by Campbell and Doeg 1989).

The lack of silvicultural effects at the drainage-basin scale on fish and macroinvertebrate assemblages seems to indicate that these systems are resistant to such perturbations. Again, this pattern may relate to the large spatial scale of this study and shifting-mosaic patterns of variability (Clark 1991, Moloney and Levin 1996). Although macroinvertebrate assemblages were more variable than fish assemblages over time (Figure 2), they were also little influenced by logging activities in these drainage basins. The sampling methods for macroinvertebrates were designed to collect predominantly in-

sect larvae. Other groups of invertebrates, such as freshwater mussels, are more impacted by these types of disturbances (Williams and others 1993, Vaughn 1997), although these organisms are more common downstream from the study areas.

Despite the apparent lack of a timber harvesting effect on the biota of these streams, harvesting activities have been shown to influence biota at smaller spatial scales (Campbell and Doeg 1989). The effects of logging on stream biota are often limited to changes in local assemblage structure (Campbell and Doeg 1989, Rutherford and others 1992). If these local changes are severe enough over time, they can manifest as more severe alterations to habitat and/or regional distribution and abundance patterns of stream organisms, but we were not able to detect such effects with these data.

We believe the lack of an association among timber harvesting and fish and macroinvertebrate assemblages relates to the widely fluctuating environmental condi-

tions of these streams (primarily hydrology) and the large, basinwide scale of this study. The effects of timber harvesting also may be very time specific, and we were not able to capture these effects with the given sampling design. There may have been postharvest effects as a response to past logging events, but the systems seem to have recovered by the time of our sampling period and showed no apparent effects. Complete pre- and post-treatment data are necessary to truly assess the effects of timber harvesting on stream ecosystems, but these data are rarely available. These results should not be generalized to other systems because basins will respond to perturbations differently depending on local and/or regional conditions, as we showed for environmental variables, and sampling scale. Because of sampling limitations, we can only address effects at the basin-wide scale. Furthermore, the timber harvesting regime in the Ouachita National Forest may be less severe than that used in other parts of the world or by other organizations or individuals that manage timber resources. Stream systems with a more "benign" natural disturbance would be more strongly affected by perturbations because of the limited natural disturbance regime (Peckarsky 1983), particularly at smaller scales. Systems with a more dynamic natural disturbance regime have some ability to recover from perturbations, but if impacts are severe enough they may interact with natural disturbance regimes to reduce the stability and diversity of these systems. In the Ouachita National Forest we did not detect such a pattern. At the basin scale, these streams seem to be maintaining natural pattern and process despite timber harvesting activities.

Most of the variation in stream biota and measured physical variables was related to basin-level factors. Variation in regional assemblage structure (taxonomic and trophic) of fishes and macroinvertebrates was strongly associated with differences among drainage basins. Thus, there were strong differences in the structure and function of regional assemblages in these individual stream basins. Such variation in the biota among streams and basins can be influenced by differences in biogeographic history, or physiography and other stream-level processes (Matthews 1987, Matthews and Robison 1988, Brazner and Beals 1997, Vinson and Hawkins 1998).

Physical stream features and regional macroinvertebrate assemblage structure varied considerably over the three years of the study, but fish assemblages varied little over time (Figure 2). Organisms that occur in hydrologically variable systems, like small Ouachita Mountain streams, have either evolved under these conditions (i.e., endemic to the system) and/or they are able to withstand the environmental extremes (Power 1992). These systems contain a number of wide-ranging generalists along with several endemic species of fishes that have the ability to withstand extremes of the natural disturbance regime. At smaller spatial scales, fish assemblages may be largely structured by colonization and extinction processes (Taylor 1997). The predicted variability in fish assemblages is not apparent for these streams at the drainage basin scale, although the assemblages may be more variable at the scale of individual stream reaches or pools.

There are a number of potential explanations for the variability of macroinvertebrate assemblages over time. Variability in stream physicochemical variables may have kept some invertebrates from reproducing and establishing populations at certain localities. Stream macroinvertebrate assemblages will be structured by both drainage basin factors and physicochemical conditions at a locality (Vinson and Hawkins 1998), and some invertebrates are particularly sensitive to environmental extremes such as droughts and floods (Delucchi and Peckarsky 1989, Grimm and Fisher 1989, McElravy and others 1989). For insects that are tied to both terrestrial and aquatic systems, adults choose breeding sites based on environmental quality at a stream site (Anderson and Wallace 1984). These organisms have the potential to freely migrate among different drainage basins, and this could provide an explanation for the strong time effects (and weaker basin-level effects, relative to fishes) on macroinvertebrate assemblages (Figure 2). Predation by fishes also influences variability of macroinvertebrate populations, particularly during periods of fluctuating water levels (Lancaster and others 1990, Dudgeon 1991, Rakocinski 1997), although this has been questioned by some authors (Allan 1978, 1982). Sampling was conducted during the summer months when these streams are often at low flow, with some pools isolated from one another. During low water periods, predaceous fishes potentially have strong effects on macroinvertebrate community structure (Dudgeon 1991) and lead to top-down trophic cascades. When pools become isolated from one another, macroinvertebrates cannot drift out of areas containing predators, and drift is an important means of predator avoidance for many of these organisms (Flecker 1992, Allan 1995). A final explanation for the variability in macroinvertebrate assemblages over time is related to the timing of samples. Within a given basin, samples may have occurred at different times during the summer, and life-cycle events (i.e., reproduction, emergence, etc.)

occurring between samples likely were responsible for some of the observed variability. Some fish species may also have reproduced during the sampling period, but because of the potential to emerge from a stream, macroinvertebrates should have higher rates of turnover leading to greater variability over time.

A fundamental question in ecology concerns how processes are linked at different spatial scales (Levin 1992) and how natural variability is dependent on scale (Lohr and Fausch 1997). At the regional scale, the factors we modeled explained 50%–70% of the variation in fish and macroinvertebrate assemblages. We plan to use generalizations derived from these data to examine how assembly patterns change with a reduction in spatial scale (i.e., individual pools). Because stream dynamics change at different spatial scales and many stream-level processes are dependent on pool-level interactions, stream pools and perhaps individual habitat types are an appropriate scale for ecological study (Matthews and others 1994, Taylor 1997). Detecting the effects of timber harvesting on stream dynamics may depend on "catching" these systems at the critical time period and spatial resolution. Although we were unable to provide a magic formula for forest managers, we were able to demonstrate that in some stream systems timber harvesting activities can be conducted without severely impacting large-scale patterns of assemblage structure. Because of their innate variability, small streams are difficult to manage (Poff and Ward 1989), and detailed studies at multiple spatial and temporal scales are necessary for their conservation. Understanding how different sources of variation contribute to the function of these systems will provide valuable information on how to manage small streams within an altered landscape.

Acknowledgments

Appendix A: Fish Species Collected by US Forest Service Inventory Teams in the Three Drainage Basins

The following table summarizes the fish species collected by US Forest Service inventory teams in the three BASS drainage basins (see Table 1). Presence of a species in a drainage basin is indicated by a '1'. The assigned trophic groups are as follows: ALG = algivore, BI = benthic insectivore, GI = general insectivore, OMN = omnivore, PIS = piscivore, SI = surface insectivore, and WCI = water-column insectivore.

Appendix A: Fish Species Collected by US Forest Service Inventory Teams in the Three Drainage Basins

Family/species	Trophic group	Basin Saline	Cossatot	Arkansas
Cyprinidae				
Campostoma anomalum	ALG	1	1	1
Luxilus chrysocephalus	GI	0	1	0
Lythrurus snelsoni	WCI	0	1	0
Lythrurus umbratilis	WCI	1	1	1
Notropis boops	WCI	1	1	1
Pimephales notatus	OMN	1	0	1
Semotilus atromaculatus	GI	1	1	1
Catostomidae				
Erimyzon oblongus	OMN	1	1	1
Ictaluridae				
Ameiurus natalis	OMN	1	1	1
Ameiurus nebulosus	OMN	0	1	0
Noturus exilis	BI	0	0	1
Noturus lachneri	BI	1	0	0
Esocidae				
Esox americanus	PIS	1	1	0
Aphredoderidae				
Aphredoderus sayanus	OMN	1	1	0
Fundulidae				
Fundulus catenatus	SI	1	1	0
Fundulus olivaceus	SI	1	1	0
Atherinidae				
Labidesthes sicculus	WCI	1	0	0
Centrarchidae				
Lepomis cyanellus	GI	1	1	1
Lepomis macrochirus	GI	1	1	0
Lepomis megalotis	GI	1	1	1
Lepomis punctatus	GI	1	0	0
Lepomis hybrid	GI	1	0	0
Micropterus dolomieui	PIS	0	1	0
Micropterus punctulatus	PIS	1	0	0
Micropterus salmoides	PIS	1	0	0
Percidae				
Etheostoma collettei	BI	1	0	0
Etheostoma radiosum	BI	0	1	1
Etheostoma spectabile	BI	0	1	1
Etheostoma whipplei	BI	1	1	1
Percina caprodes	BI	1	0	0

Appendix B: Macroinvertebrate Taxa Collected by US Forest Service Inventory Teams in the Three Drainage Basins

The following table summarizes the macroinvertebrate taxa collected by US Forest Service inventory teams in the three BASS drainage basins (see Table 1). Presence in a drainage basin is indicated by a '1.' The assigned trophic groups are as follows: CF = collector-filterer, CG = collector-gatherer, CO = commensal, NF = non-feeding, PI = predator-piercer, PR = predator-engulfer, SC = scraper, and SH = shredder.

Appendix B: Macroinvertebrate Taxa Collected by US Forest Service Inventory Teams in the Three Drainage Basins

Order/family (No. genera)	Trophic group	Saline	Cossatot	Arkansas
Gastropoda				
Ancylidae (1)	SH	1	0	0
Planorbidae (1)	SH	1	0	0
Bivalvia				
Sphaeriidae	CF	1	0	0
Nematomorpha	NF	0	1	0
Oligochaeta	CG	1	1	1
Branchiobdellida	CO	1	1	1
Hirudinea	PA	1	1	0
Amphipoda				
Crangonyctidae (2)	CG	1	0	1
Talitridae (1)	CG	1	1	1
Isopoda				
Asellidae (2)	CG	1	1	1
Decapoda				
Astacidae	CG	0	1	0
Cambaridae (2)	CG	1	1	1
Hydrachnida				
Hydrachnidae	PR	1	1	1
Gollembola	CG	1	1	0
Ephemeroptera				
Baetidae (3)	CG	1	1	1
Caenidae (1)	CG	1	1	1
Ephemerellidae (2)	CG	0	0	1
Ephemeridae (2)	CG	0	1	0
Heptageniidae (4)	SC	1	1	1
Leptophlebiidae (3)	CG	1	1	1
Isonychiidae (1)	CF	0	1	0
Leptohyphidae (1)	CG	1	1	0
Odonata				
Aeshnidae (1)	PR	1	1	1
Calopterygidae (2)	PR	0	1	0
Coenagrionidae (2)	PR	1	1	1
Corduliidae (3)	PR	1	1	0
Gomphidae (3)	PR	1	1	1
Libellulidae (1)	PR	1	1	0
Plecoptera				
Capniidae (1)	SH	0	1	0
Leuctridae	SH	1	1	1
Nemouridae (1)	SH	0	0	1
Perlidae (5)	PR	1	1	1
Hemiptera				
Corixidae (2)	PI	1	0	1
Gerridae (4)	PI	1	1	1
Mesoveliidae (1)	PI	0	1	0
Notonectidae (1)	PI	1	1	1
Saldidae (1)	PI	1	0	0
Veliidae (2)	PI	1	1	1
Megaloptera				
Corydalidae (2)	PR	1	1	1
Sialidae (1)	PR	1	1	1

Appendix B: Macroinvertebrate Taxa Collected by US Forest Service Inventory Teams in the Three Drainage Basins

Order/family (No. genera)	Trophic group	Saline	Cossatot	Arkansas
Trichoptera				
Glossosomatidae (1)	SC	0	0	1
Helicopsychidae (1)	SC	0	1	0
Hydropsychidae (4)	CF	1	1	1
Lepidostomatidae (1)	SH	1	1	1
Leptoceridae (2)	CG,PR	1	1	0
Limnephilidae (2)	SC,SH	1	0	1
Philopotamidae (2)	CF	1	1	
Philopotamidae (2)	CF	1	1	1
Polycentropidae (1)	PR	1	1	1
Psychomyiidae (1)	SC	0	1	0
Rhyacophilidae (1)	PR	1	1	1
Lepidoptera				
Pyralidae (1)	SH	1	1	0
Tortricidae (1)	SH	0	0	1
Coleoptera				
Curculionidae (1)	SH	1	0	0
Dryopidae (1)	SH	1	1	1
Dytiscidae (7)	PI,PR	1	1	1
Elmidae (5)	CG	1	1	1
Gyrinidae (1)	PR	1	1	1
Hydrophilidae (4)	PI,PR	1	1	1
Psephenidae (2)	SC	1	1	1
Staphylinidae (1)	PR	0	1	1
Diptera				
Ceratopogonidae (2)	PR	1	1	1
Chironomidae (35)	CG,PR,SH,CF,SC	1	1	1
Culicidae (1)	CF	1	0	0
Dixidae (2)	CG	0	1	1
Empididae (1)	PR	1	1	1
Muscidae (1)	PI	0	0	1
Phoridae	PR	1	0	0
Simuliidae (2)	CF	1	1	1
Tabanidae (4)	CG,PI	1	1	1
Tipulidae (5)	PR,SH,CG	1	1	1

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